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Influence of Climate on the Distribution of Walruses, *Odobenus rosmarus* (Linnaeus). II. Evidence from Physiological Characteristics.

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(Text-figures 1-9)

INTRODUCTION

THE principal objective of this and the foregoing study (Fay & Ray, 1968) was to test the theory first expressed by von Baer (1838) that walruses are prevented by warmer climates from extending their range southward. The rationale was that walruses are closely adapted to the environment they occupy; that they are highly mobile and could readily move farther southward; that no physiographic barriers prevent them from doing so, therefore they must be inhibited by nonadaptation to some physical or biotic factors of the more southerly environments. Upon comparing the principal physical and biotic characters of their range with those of areas immediately to the south, we concluded that climate was the most probable restrictive factor. We and others have observed that, under certain conditions, walruses and some other pinnipeds seem to be sensitive to extremes of atmospheric and solar heat.

The influence of climate on the distribution of animals has usually been evaluated indirectly by correlating climatological data with the altitudinal or latitudinal range of species (see review by Allee, *et al.*, 1949). We have taken a more direct

course by examining the specific reactions of individual animals to climatic and microclimatic conditions. Walruses are adapted to the water of the polar sea, which in terms of cooling power is one of the coldest environments on earth. That they are highly efficient at conservation of body heat is indicated by their ability to sleep in the cold water. However, they also spend a large part of their time out of the water, where they are exposed to a greater variety of thermal conditions, the warmest and coldest of which evoke behavioral signs of thermal stress, considered in our previous paper. In this paper we report some physiological responses associated with the observed behavior.

The physiological thermoregulation of pinnipeds has been studied in recent years principally by Irving and associates (Irving, *et al.*, 1935; Scholander, 1940; Scholander, *et al.*, 1950a, 1950b; Irving & Hart, 1957; Hart & Irving, 1959; Irving, *et al.*, 1962), largely using restrained animals to facilitate measurement of physiological characteristics. These animals were exposed mostly to controlled environments, adequately described by ambient temperatures alone. The results indicated the animals' capability for maintaining a constant internal temperature exclusively by physiological means, but they did not describe the total thermoregulatory responses of the free-living animal nor take into consideration the complex thermal conditions of the natural environment.

In this study, we worked mostly with animals that were free to react to weather in their natural environment or in their quarters at the New York

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Aquarium. In doing so, we hoped to gain insight into the interrelationships of behavior and physiology in thermoregulation, particularly as they interact near the upper limits of the "tolerance zone." This zone is defined as comprising the range of weather conditions tolerated by pinnipeds while at rest in air. When its limits are exceeded, the animals withdraw to the water (Fay & Ray, 1968).

MATERIALS AND METHODS

The wild animals studied were 14 adult and subadult Pacific walrus, *O. r. divergens* (500 to 1560 kg), in the vicinity of St. Lawrence Island, Bering Sea, and Round Island, Bristol Bay, Alaska. Data on captive animals were obtained from a juvenile male Atlantic walrus, *O. r. rosmarus* (age four to five years, weight 500 to 600 kg), and a young female Pacific walrus (age one month to two years, weight 54 to 254 kg) at the New York Aquarium. Data from calves were obtained from 11 newly captured animals (ages one day to two months, weights 59 to 73 kg) at Gambell, Alaska, at the Woodland Park Zoo in Seattle, and at the New York Aquarium, Coney Island, New York.

All data from wild adults and subadults were obtained from animals that were at rest when killed by rifle, mostly during the course of an Eskimo hunt. Data from juveniles and calves were obtained on living animals while they were at rest and free to respond behaviorally to the ambient conditions. Rectal temperatures were taken at depths of 15 to 20 cm with mercury rectal thermometers or Weston dial thermometers that had been standardized at 37°C. All other temperatures were taken with the latter. Subsequent checks against telethermometers (YSI) showed close agreement with Weston thermometers, the chief difference being time to reach equilibrium. Body skin temperatures were

measured on the lateral, ventral, or dorsal aspect, whichever was driest and most distant from the substrate. Flipper temperatures were taken on the webbing of the rear flippers about midway between the tarsals and the tip.

Breathing and heart rates were counted on resting animals, mostly coincident with measurements of skin temperature. Breathing was observable by nostril action, sound, or chest inflation. Heart action was detected visually or by axillary palpation.

Data from wet and dry animals were treated separately. In all cases, ambient weather was recorded at the site and level of the animal and at the same time as physiological or behavioral observations.

RESULTS

Internal Temperatures

The mean body core temperature (thoracic cavity) of ten subadult and adult walrus in an ambient temperature range of -1 to 14°C was 36.6°C, or about 1.2°C lower than the mean for terrestrial mammals of a similar size (Morrison & Ryser, 1952). Rectal temperatures of the same walrus were nearly identical to the core temperatures (Table I). The rectal temperatures of calves were significantly higher than those of the subadults and adults, averaging 37.5°C. Some of the highest temperatures were measured in teething calves in temperate climates, and it is conceivable that temperatures were elevated as a result of that condition. We also suggest that the warmer conditions of captivity induced higher rectal temperatures, but our data from calves in cold conditions are too few to show this. A diurnal fluctuation of body temperature also was suggested. The mean rectal temperature of five calves in midmorning was $38.2 \pm 0.29^\circ\text{C}$, whereas in the same calves in late afternoon it was $37.8 \pm 0.18^\circ\text{C}$.

TABLE I
INTERNAL TEMPERATURES OF RESTING
WALRUSES AT AIR TEMPERATURES OF -1 TO 25°C

Age of Animals	No. Observations	Thoracic Temperature °C		Rectal Temperature °C	
		Range	Mean \pm S.E. _m	Range	Mean \pm S.E. _m
1-6 months	36	35.3-39.0	37.5 \pm 0.13
	1	37.0
1-3 years	1 ^a	36.2
> 5 years	10	34.0-38.0	36.2 \pm 0.42
	10	34.0-38.0	36.6 \pm 0.32

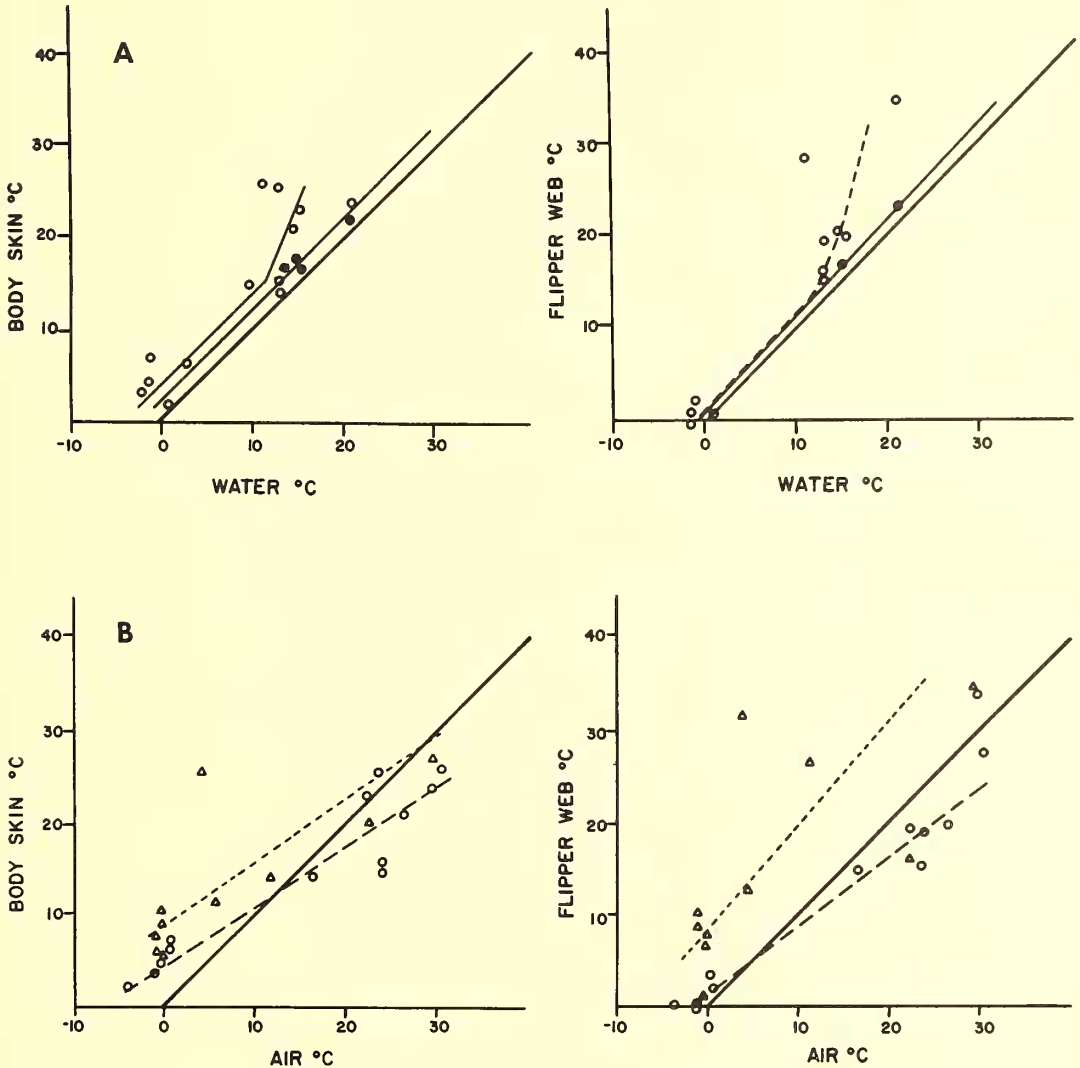
^aData from Rausch, unpublished.

Temperature of the Skin When Wet

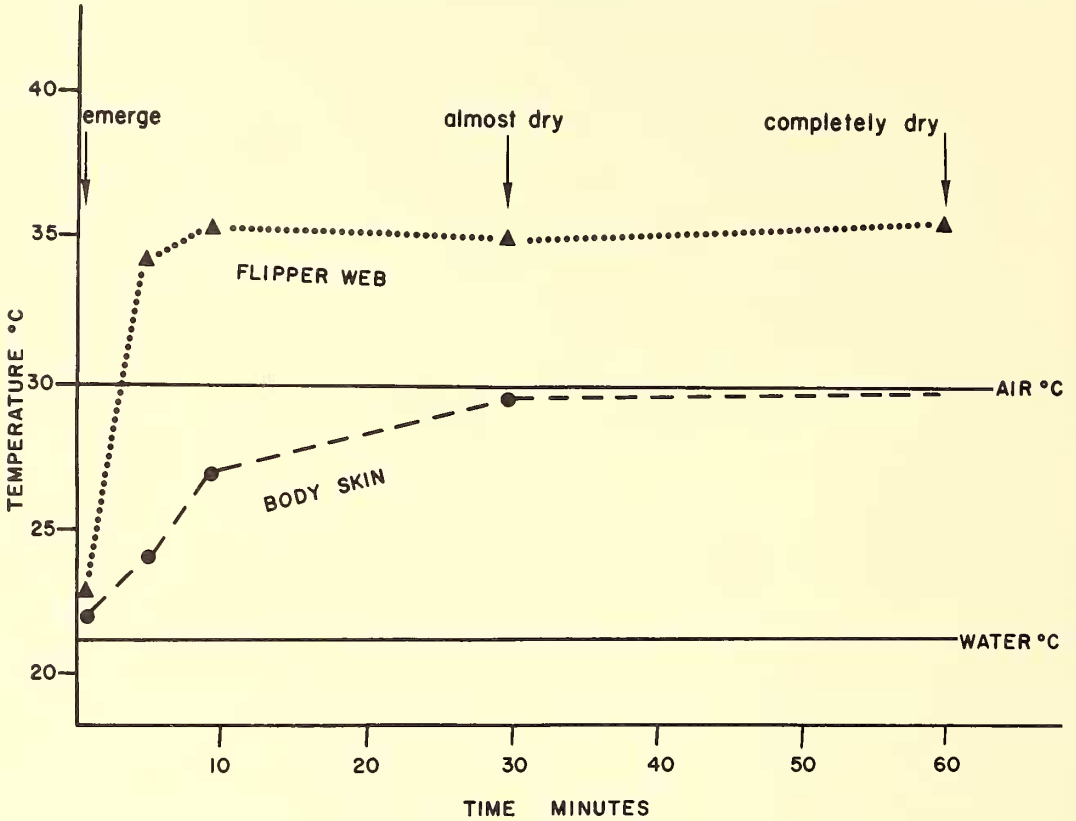
The body surface and flippers of moderately active animals during immersion were 1 to 3°C warmer than the water (Text-fig. 1A). This finding is in accord with those of other workers (Irving & Hart, 1957; Hart & Irving, 1959; Ray & Smith, 1968) and indicates that, whether restrained or not, pinnipeds are usually about as cool on the body surface as the water in which they are immersed.

For at least five to 10 minutes after emerging

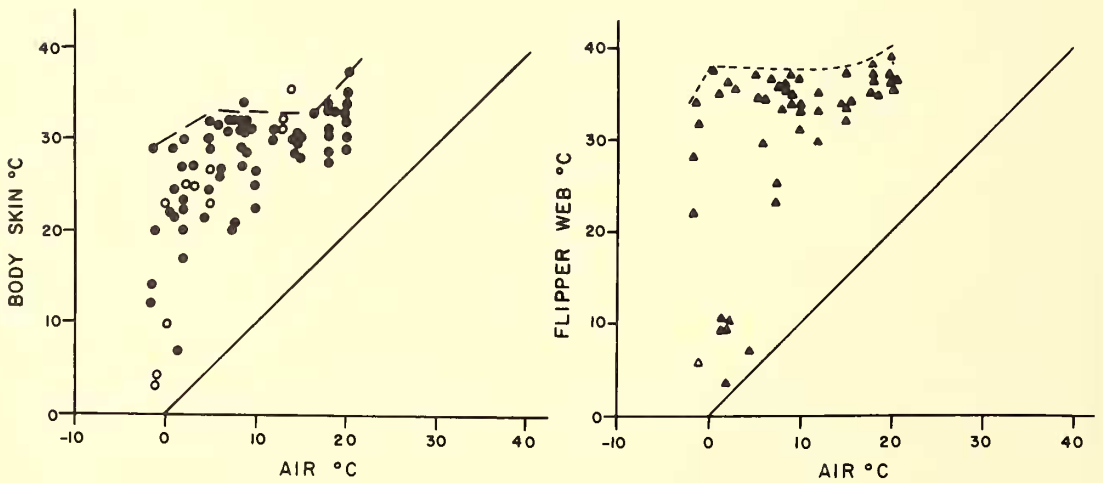
from the water, the walrus remained cool on the body surface, usually within 8°C of the water temperature, provided that the water was cooler than 10°C and the air cooler than 20°C. The body surface warmed more rapidly when air and water temperatures were high, and the temperature of the flippers rose faster and more erratically than did that of the body skin (Text-fig. 1B). Within an hour after emergence, the skin of the body and flippers was usually dry and had attained a relatively stable temperature, most



TEXT-FIG. 1. Temperatures on the skin of the body and rear flipper web of walrus: (A) in water —●— and immediately after emergence into air —○—, (B) in air within 10 minutes —○— and within 20 minutes ---△--- after emergence.



TEXT-FIG. 2. Example of the rate of warming of the body skin and rear flipper web of a captive juvenile female walrus from the time of emergence into air until the skin was dry.



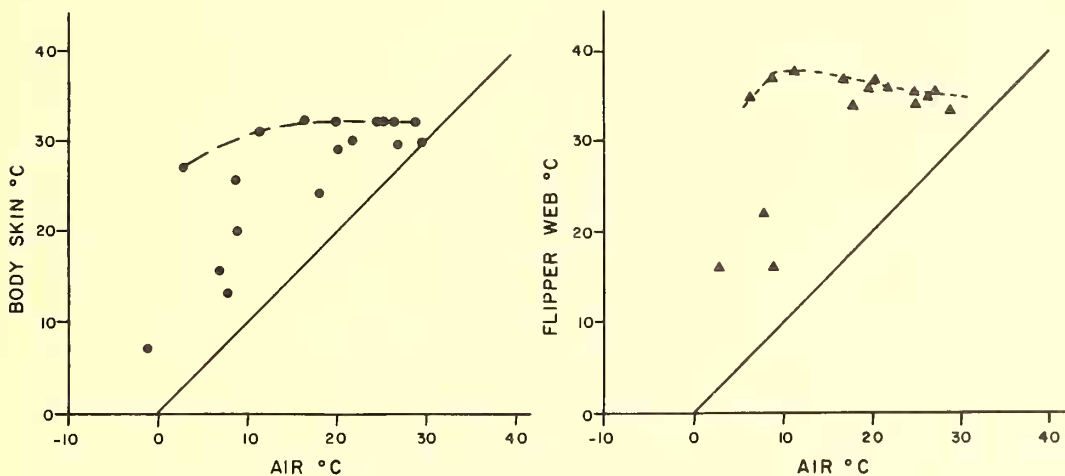
TEXT-FIG. 3. Temperatures of the dry skin of the body and rear flipper web of newly captured calves and wild adult walrus at rest in air. ● ▲ = newly captured calves. ○ △ = wild adults. Curves delimit the usual upper limits of temperature.

often higher than that of the air. The role of the flippers in the dissipation of heat is indicated by the high temperatures attained by them, especially in air warmer than body skin temperature. (Text-fig.2).

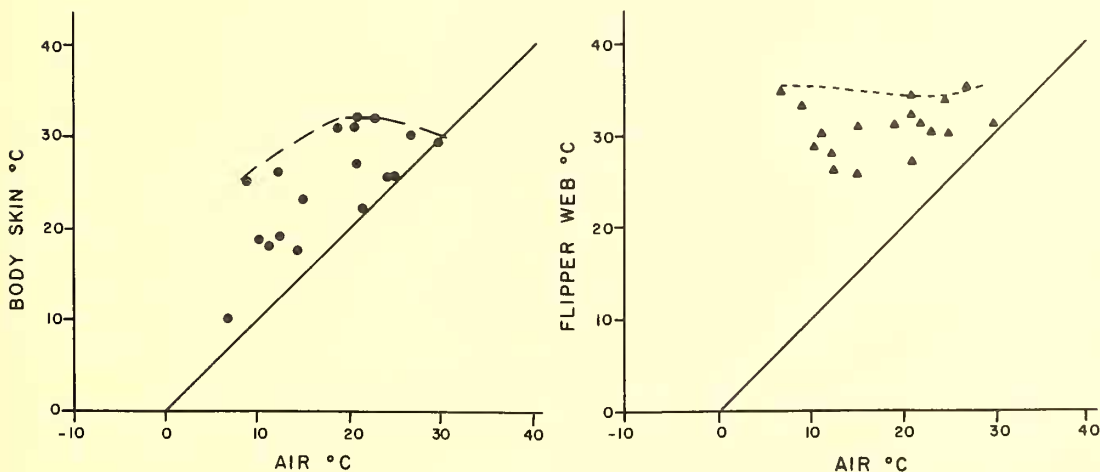
Temperature of the Skin When Dry

At air temperatures from 0°C, to about 15°C, the temperature of the dry skin on the body of wild calves and adults was usually higher than 20°C but rarely higher than 32°C (Text-fig. 3). The latter seemed to be an upper "limit," beyond which the skin temperature ordinarily did not rise. Thus, the skin/air temperature curve of

wild walrus flattens out to a "plateau" in the range from near freezing to about 15°C; at higher air temperatures, the curve again rises steeply. This plateau was evident also in the captive walrus at the New York Aquarium, within a higher range of ambient temperatures (Text-figs. 4-5) and has not been noticed previously in pinnipeds, perhaps because it does not occur in restrained animals or occurs in them over a narrower range of ambient temperatures (cf. Irving & Hart, 1957). It was detected recently in unrestrained Weddell seals (Ray & Smith, 1968), and we have also observed it in other unrestrained pinnipeds at rest (unpublished). Eleva-



TEXT-FIG. 4. Temperatures of the dry skin of the body and rear flipper web of a juvenile female walrus at the New York Aquarium. Curves delimit the usual upper limits of temperature.



TEXT-FIG. 5. Temperatures of the dry skin of the body and rear flipper web of a juvenile male walrus at the New York Aquarium. Curves delimit the usual upper limits of temperature.

tion of skin temperature above the 32°C plateau coincided in calves and adults with the first behavioral signs of heat stress (Fay & Ray, 1968).

Under most conditions, the flippers were somewhat warmer than the surface of the body and showed an even greater tendency for sustained high temperature over a wide range of air temperatures (Text-figs., 3-5). In air warmer than 0°C, the flippers were usually between 30 and 37°C; they were cooler than 25°C only when wet or in contact with ice or snow. Brief, spontaneous fluctuations of 5 to 6°C in flipper temperature were detected at ambient temperatures lower than 10°C, and fluctuations of 2 or 3°C were occasionally detected at higher air temperatures.

The temperature of the calves' flippers rose above the 37°C level only in air warmer than about 15°C, i.e., at or about the same ambient temperatures in which the skin of the body exceeded the 32°C plateau and signs of heat stress first appeared. The occurrence of flipper temperatures of 38 and 39°C might have been indicative of rising internal temperature, such as could occur with increased metabolism or inadequate dissipation of heat.

Calves resting in air warmer than 15°C and adults in air warmer than 10°C showed a distinct reddish cast on the body and flippers, in contrast to the normal pallor of animals under cooler conditions. Pale adults killed when the air was -20 to 5°C were usually cool to the touch and their skin and flippers scarcely bled at all when slashed. Reddish adults killed in air of 13 to 14°C were contrastingly hot to the touch and bled profusely when slashed. When these hot animals were thoroughly bled out, their skin became as pale as the cool animals', demonstrating that the redness and heat were due to vasodilation and the resulting hyperemia. This hyperemic condition has often been called sunburn in popular literature.

The contrast between hyperemic and ischemic animals was especially noticeable at Round Island, where most of the animals were in a nearly hairless stage of their annual molt. When in the 10°C water, the lightly pigmented adults appeared nearly white, whereas they became reddish after lying out on the beach for an hour or more. When these reddish animals were chased back into the water, their skin at once regained its pallor.

Breathing and Heart Rates

Both breathing and heart rates appear to be highly variable, even in resting calves. Minimum breathing rates in calves exposed to stepwise increases of still air temperature in shade declined from 16 per minute at -1°C to 4 per minute at

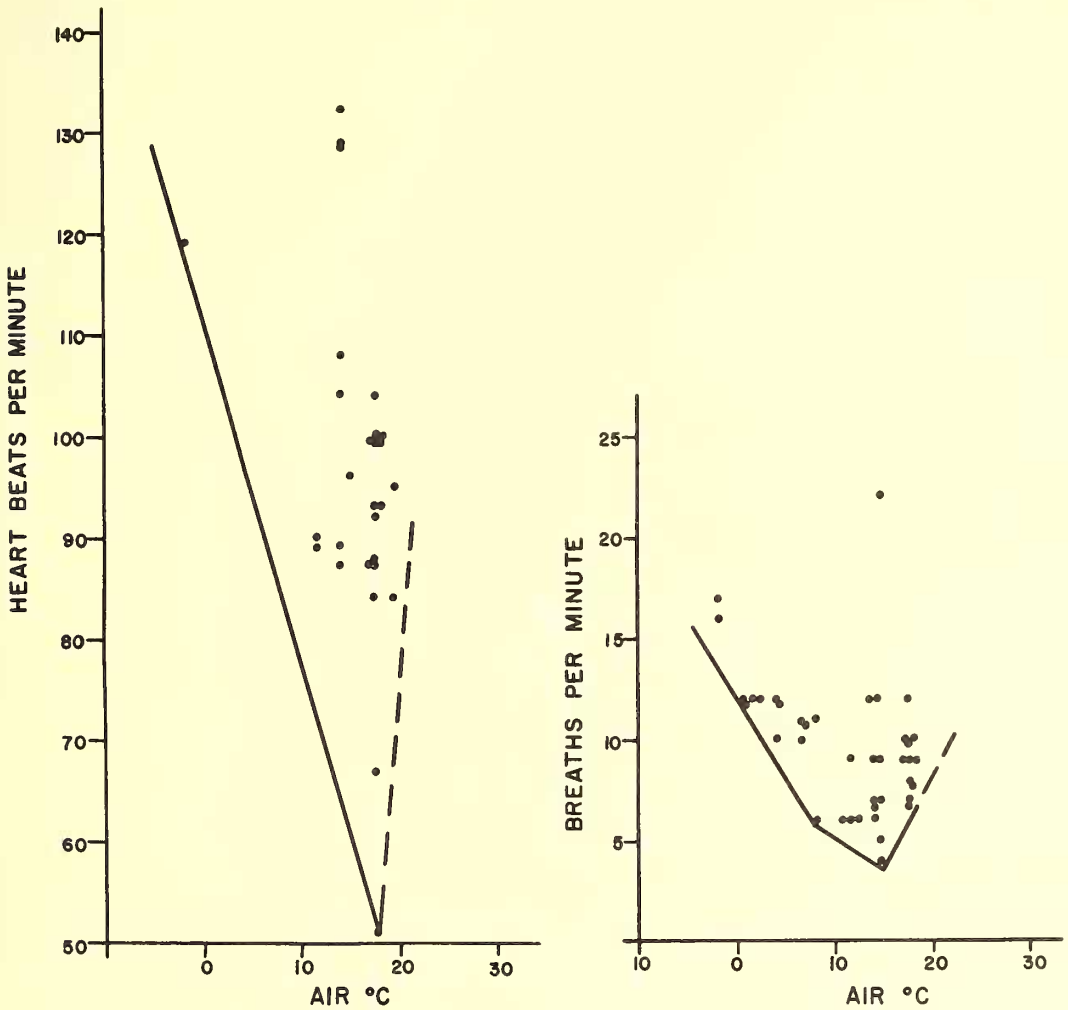
15°C, and rose again to 7 per minute at 18°C (Text-fig. 6). These rates include brief periods of apnea, especially prevalent at 10 to 18°C, and each point in the graph represents the mean of several counts. We did not notice panting under any conditions. Minimum heart rates in the same animals declined from 119 to 52 per minute in the same temperature range, though rates as high as 133 per minute were recorded at about 15°C. Lacking any special equipment for measuring heart rates, we were usually unable to determine them at ambient temperatures lower than 5°C or even 10°C due to the animals' frequent violent shivering. Since these were animals destined for display at the aquarium, we did not expose them to temperatures higher than 19°C, at which they already appeared distressed.

Temperature Gradients in the Skin and Blubber

Temperatures of the tissues were measured at several depths up to 20 cm in a few adults immediately after they were killed. Some of these animals were dry and on land or ice; others were wet and on ice. Relatively steep temperature gradients were indicated in most cases, and these were taken up mainly in the skin and blubber (Text-fig. 7). Their lengths, taking the inner end point to be 0.5°C lower than the deep thoracic temperature (Irving & Hart, 1957), ranged from near 0 cm to about 15 cm. Compared with the gradients measured in smaller pinnipeds (Hart & Irving, 1959), these were much longer and were not correlated in the same way with the internal temperature-skin temperature difference. We assume that these dissimilarities were due to the greater thickness of the walrus' skin and blubber, which should be expected to accommodate a longer gradient if the tissues are effective as insulation.

The shortest gradient amounted to virtually no gradient at all. This was measured in an adult male lying on a rocky beach in sunshine when the air was 14°C (Text-fig. 7I). The surface and cutaneous tissues of this specimen were about as warm as the interior of its body. Under similar conditions but without sunshine, two other adults had surface temperatures 5 to 7°C lower than that of the body core (Text-figs. 7G, H). We attribute the greater superficial warmth of the first animal to solar radiation. For example, a mercury thermometer and a Weston dial thermometer exposed to the sun registered 22 and 34°C, respectively, and the surface of a walrus cadaver nearby was 40.5°C. Thus, the length of gradient is not purely a function of air temperature.

We were not equipped to measure temperature gradients in the living calves and had no opportunities otherwise to determine the form of



TEXT-FIG. 6. Heart and breathing rates of newly captured walrus calves with relation to ambient still air temperature in shade.

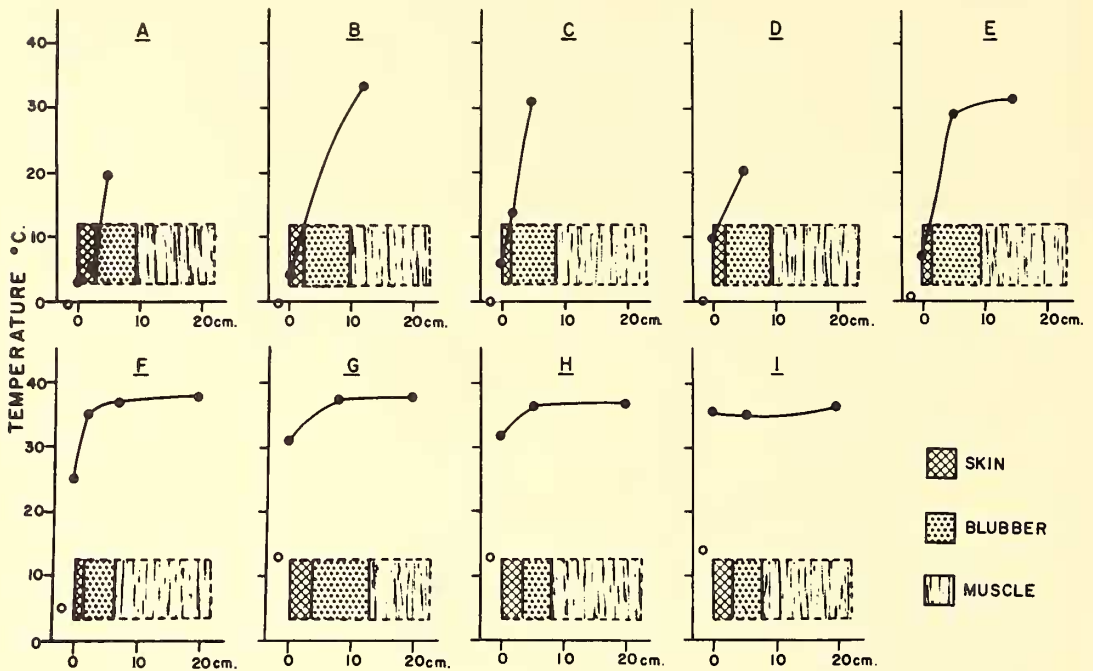
such gradients. Although the calves were about twice as large as young harbor seals, such as those used by Irving and Hart (1957), the thickness of their insulation (skin and blubber) was about the same. Therefore, we assume that the temperature gradients in their tissues were comparable to those of the seals, since gradient length seems to be as much a function of the thickness of the insulation as of the internal temperature-skin temperature difference.

DISCUSSION

Correlation of Thermoregulatory Behavior and Physiology

The walrus is a homeothermic mammal with an internal temperature of about 36.6°C, probably intermediate between those of other small-

er and larger pinnipeds (Bartholomew, 1954; Bartholomew & Wilke, 1956). We assume that this temperature is maintained in a balance between heat production and heat loss and that the production of metabolic heat is usually at the basal level in resting walruses, whether in or out of the water. The loss of heat is closely regulated by vasomotor and behavioral means, within the limits imposed by the animal's surface-to-volume ratio and amount of physical insulation (hair, skin, and blubber). We have described in the previous paper the behavioral adjustments that walruses make in response to their thermal environment, and we report here some indices of their physiological adjustments. Most of our information was obtained from very young animals, up to one or two months old. From their behavior alone, it was clear that these infants



TEXT-FIG. 7. Temperature gradients in the superficial tissues of adult wild walrus within a few minutes of death. Skin and blubber thicknesses at the site of measurement are drawn to scale (thinner-skinned animals are females). Air temperatures within 1 meter of the body are indicated by open circles to the left of each section. A-D were wet and E-I were dry animals.

were not yet fully adapted to even the moderate cold of the arctic springtime, but that they had about the same tolerance of heat as the adults. By correlating their physiology and behavior (Text-fig. 8), we obtained a useful model with which the adults' reactions could be compared.

The calves resting in air at -1 to 3 or 4°C assumed a tense fetal posture (minimum exposure of surface) and shivered violently (Text-fig. 8). At the same time, the temperature on the surface of the almost-dry to dry body ranged from 7 to 30°C and similarly on the flippers from 22 to 37°C . Breathing and heart rates were the highest recorded at any temperature, and an elevated metabolic rate was also indicated by the intense shivering. Adults under similar conditions showed comparable skin temperatures but were clearly more comfortable and relaxed.

We have seen that adult walrus readily expose themselves to air temperatures as low as -20°C with light winds (Fay & Ray, 1968), and they are known to lie in the open occasionally in much colder weather (Freuchen, 1935).

The calves continued to shiver intermittently up to an ambient temperature of 7 or 8°C but

only occasionally at temperatures of 10°C or more. Their posture became more relaxed, and there was a significant decline in the breathing rate. Between 10 and 15°C , they became fully relaxed and lay on their back or sides with flippers limp and away from the body. Adults under comparable conditions behaved in the same way, and their skin temperatures, like the calves', were sustained at 25 to 32°C ; the flippers of the calves were sustained at 30 to 37°C , i.e., near or at the temperature of the body core.

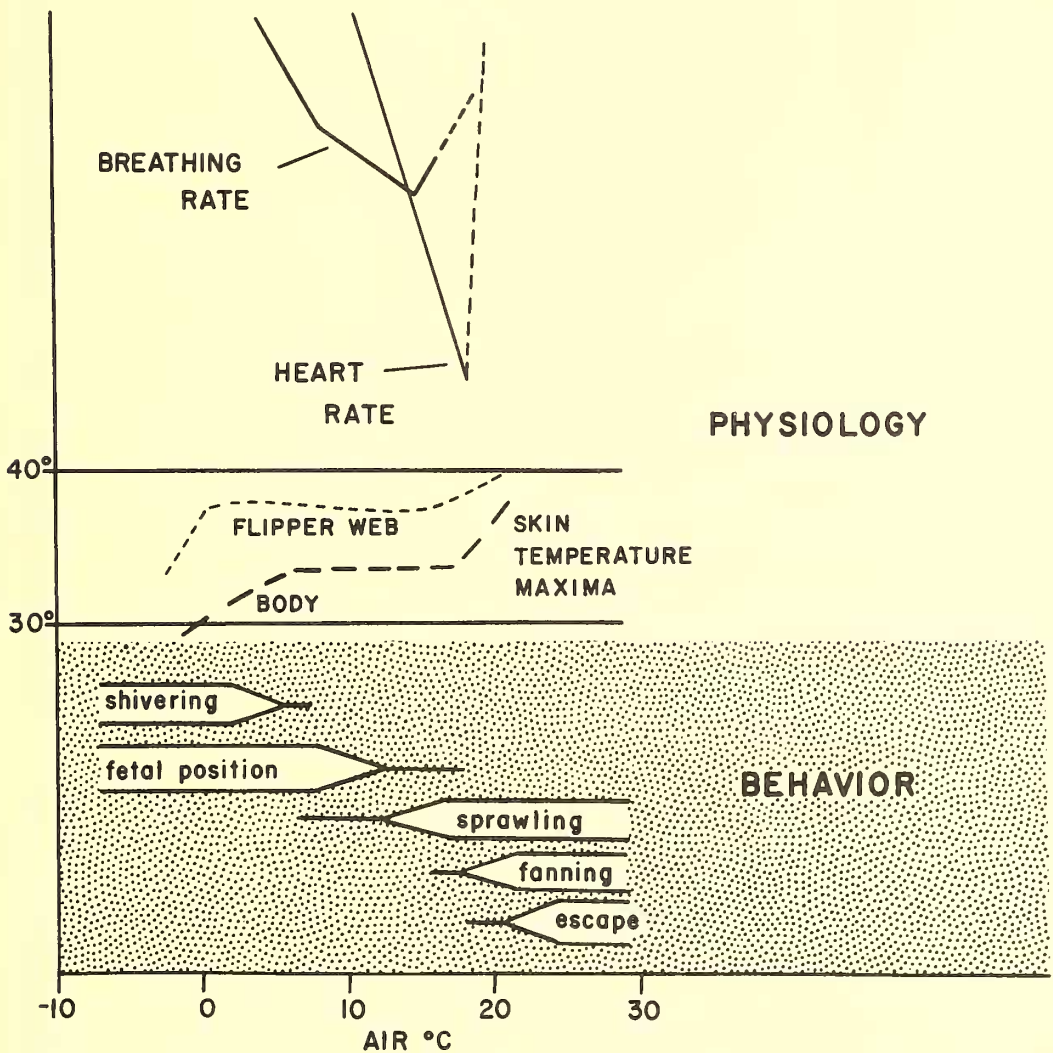
Breathing rates of the calves declined to the lowest recorded levels at an air temperature of about 15°C , and minimum heart rates occurred at 18 to 20°C . The calves, in general, became restless at the latter temperatures, sprawling for maximum exposure of surface and fanning with the fore flippers. At this point also, skin and flipper temperatures rose above the previously sustained levels, indicating a major increase in heat output and, we think, of heat production. Ultimately, when air temperatures reached more than 20°C the calves "escaped" into the water, where they sometimes resumed their sleep.

The behavioral reactions of adult walrus

under comparably warm conditions were virtually the same as those of the calves. Sprawling and fanning were observed when they lay out in air at 8.5°C with intense midday insolation and no wind (latitude 66°, mid-May), and at 14°C with afternoon sun and 2-mps breeze (latitude 58°, mid-June). Conditions warmer than the latter are uncommon in the walrus' range but common to the south of it, where insolation is more intense and air temperatures generally higher.

The captive juveniles, with a history of one to five years' exposure to the temperate climate of Coney Island, New York, responded behavior-

ally in a pattern comparable to the calves'. They did not haul out often in air cooler than 3 or 4°C or warmer than 25°C, and when they did emerge under these conditions, they stayed for only a short time, usually returning to the water before their skin dried off. However, under most conditions, their skin was cooler than that of the calves, and in no case did their skin or flipper temperatures rise above the usually sustained levels. We assume that these differences reflect physiological maturation and acclimatization to temperate climate, with more efficient conservation of heat in cold weather and better dissipation of heat when the weather was warm.



TEXT-FIG. 8. Correlation between characteristic physiological and behavioral responses of newly captured walrus calves and ambient still air temperatures in shade.

Limits of Thermoneutrality and Thermal Tolerance

Without actual measurements of metabolic rates, we could not determine the exact limits of thermoneutrality in either the calves or the adults, but the indirect evidence was strongly suggestive of some general parameters. From the calves' highly variable skin and flipper temperatures, high breathing and heart rates, and, especially, intensive shivering at still air temperatures of 5°C and lower, we estimate that the lower limit (= critical temperature) of their thermoneutral zone was probably about 5°C. Their shivering alone was indicative that metabolism was increased above the basal rate. For adults, the critical temperature is assumed to be much lower, but we do not know how low. Judging from their ostensible comfort at air temperatures near -20°C with light wind, we are confident that they can withstand at least that much cold without elevation of their metabolism.

We estimate that the upper limit of thermoneutrality for the nonacclimatized calves was at or near 18°C in still air and shade. This was based on analogy with other homeotherms, in which minimum breathing and heart rates occur usually at or near the upper limit of thermoneutrality (e.g., Bartholomew & Hudson, 1962; Hudson & Brush, 1962; Hudson, 1965), and elevated body temperatures are correlated with increased metabolism (e.g. Graham *et al.*, 1959; McNab & Morrison, 1963). Elevation of body temperature in the walrus calves was indicated by the rise of flipper temperature above 37°C at air temperatures over 18°C, for the flippers could not have become warmer than the normal body core unless the core temperature itself had risen. Also possibly indicative were the high rectal temperatures recorded occasionally from calves introduced to temperate climate.

The upper limit of thermoneutrality for adults is unknown but is believed to be similar to that of the calves. This is suggested principally by their comparative behavior (Fay & Ray, 1968). Adults at the southern edge of their geographic range in summer, in 14°C air with sunshine and light breeze, showed signs of heat stress (hyperemia, sprawling, restlessness, fanning) comparable to those in calves in still air and shade at 18°C or more. The added heat from the sun in that situation was equivalent to at least an additional 10°C of air temperature and was only partly counterbalanced by the breeze. From their behavior, we judged that the majority of these animals would not have tolerated much warmer weather. A high proportion of them had already withdrawn into the sea.

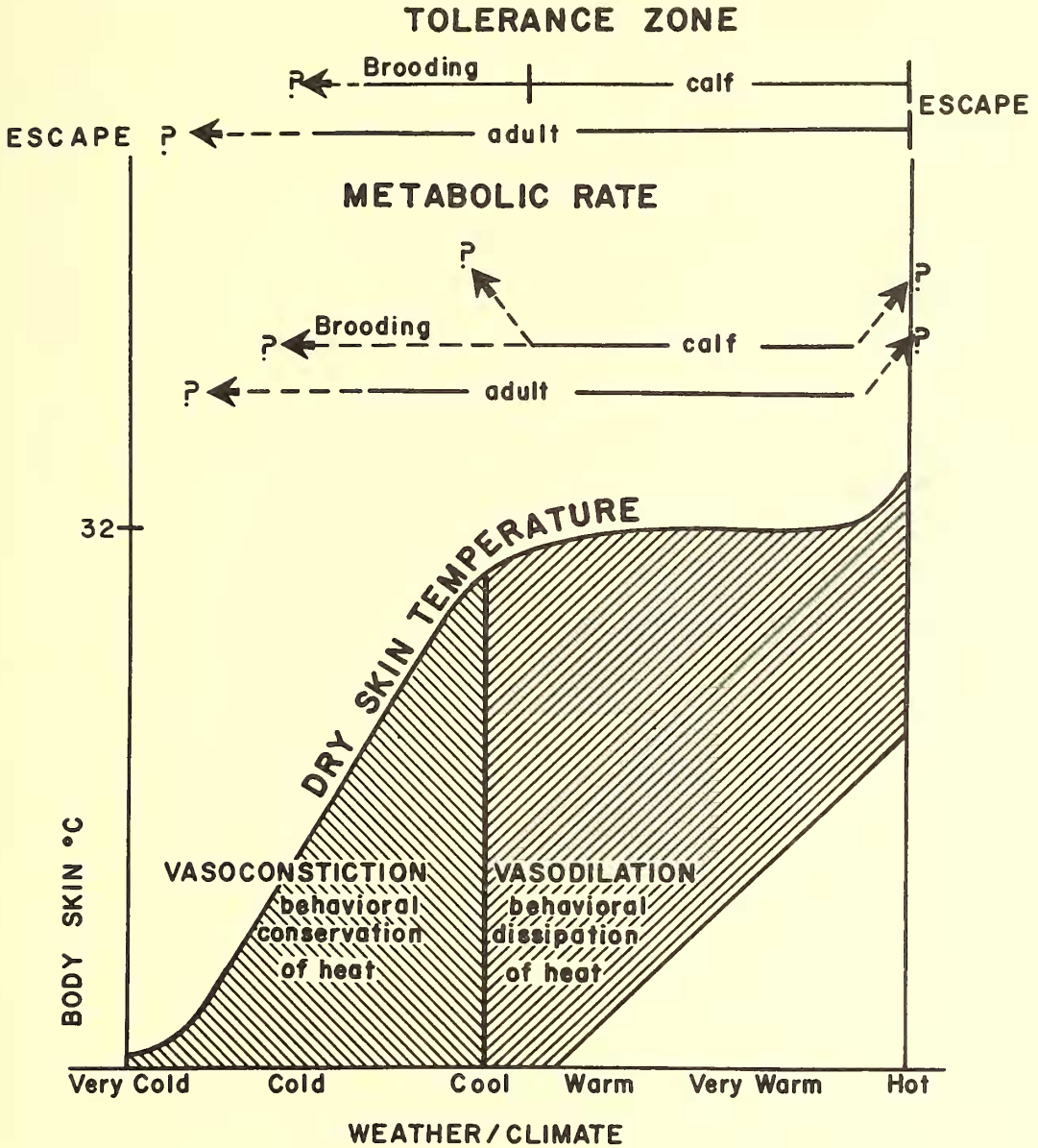
The general scheme, as we envision it, of wal-

ruses' reactions to the thermal climate in air is shown in Text-fig. 9. Here, the scale of thermal conditions (abscissa) is necessarily vague because individual animals will be influenced not only by air temperature but by wind, solar radiation, moisture, and the conductivity of the substrate. These combine to present an "effective" temperature that could not be considered in detail here (cf. Ray & Smith, 1968).

Their reactions may also vary with individual and seasonal differences in acclimatization, the thickness of their insulation, their maternal status, the molt, and their general physical and nutritional condition. Molting animals seem to be more sensitive to cold and less sensitive to heat than any others; cows with newborn calves and sick or exhausted animals tend to be least sensitive to either. Tolerance will vary also with the number of animals in the group. Large herds can be expected to tolerate more intense cold than isolated animals because of their huddling and mutual improvement of the microclimate. Conversely, huddling groups will be less tolerant of heat because of their reduced surface area. Indeed, the gregariousness and persistent huddling of walrus may be among the most influential factors determining the limits of their thermal tolerance.

The limits of tolerance are shown as being somewhat wider than the estimated limits of thermoneutrality. This is based mainly on the reactions of the calves, in which escape evidently was not induced until the metabolism had risen above the basal level. In the captive juveniles and the adults, the two zones may have coincided exactly. We believe that wild walrus usually avoid exposure to conditions outside of their thermoneutral zone and that the principal function of the escape reaction is the withdrawal from unfavorable conditions. Whereas the attainment of thermoneutrality may often be feasible in air, it probably is always feasible in the water in healthy animals due to the normal condition of vasoconstriction.

The question of why walrus haul out at all, if they can sleep in the water with minimum production of heat, may be answered by considering the metabolic requirements of their skin. For conservation of body heat during immersion, the skin is permitted to cool to about the same temperature as the water and is largely deprived of blood due to vasoconstriction. The epidermis, which comprises the outermost layer, in direct contact with the medium, is most affected. At the low temperatures normally sustained during immersion, the epidermis is evidently in a semidormant state and is incapable of performing its growth and reparative func-



TEXT-FIG. 9. Schematic representation of dry skin temperature and its relation to the tolerance zone and metabolic rate of walruses at rest in air. The critical physiological limits are not known for the walrus, nor are the exact points of escape with response to extreme low temperature. Thermoneutrality is predicted within the entire tolerance zone and is considerably extended in calves by maternal brooding (Fay & Ray, 1968). Acclimatization has the effect of shifting these predicted responses.

tions (Feltz & Fay, 1967). The optimum temperature for epidermal growth seems to be near 30°C, which is attainable in the skin of polar pinnipeds only when exposed to the air. By means of behavioral regulation of their surface area and its exposure to the air, walruses are

capable of sustaining the required skin temperature under a wide variety of climatic conditions. This is reflected in the plateauing of the skin/ambient temperature curve in the upper half or more of the zone of thermoneutrality.

The highest dry skin temperature on the body

during thermoneutrality is about 32°C. When this temperature is exceeded, walrus become restless, begin fanning, and ultimately withdraw into the water. We have seen that this occurs, mostly in huddling walrus, even in the relatively cool climate at the southern edge of the walrus' range, and we believe that warmer climates would be intolerable for this reason alone. Provided that these animals would retain their usual pattern of diurnal rest and nocturnal activity, as well as their thigmotactic and heliophilic behavior, we are confident that they could not reside in comfort at lower latitudes in summer. Walrus exposed to temperate climates while in captivity successfully avoided hyperthermia during the warmest weather by hauling out only so long as they were cooled by evaporation, or by hauling out at night. (Fay & Ray, 1968). However, because of their diurnal feeding schedule in captivity, they were not as closely bound to the normal activity rhythm. Some ancestral walrus evidently lived in warmer climates than their modern descendants (Ray, 1960; Mitchell, 1961, 1962), and the morphology of at least one of these suggests that it led a more pelagic existence.

SUMMARY AND CONCLUSIONS

1. The influence of climate on the distribution of walrus was investigated by measuring some parameters of physiological thermoregulation in unrestrained animals at rest, under natural and controlled conditions at ambient temperatures from -1 to 25°C. Data were obtained on the temperatures of the body core, skin, and hind flippers and on the breathing and heart rates and temperature gradients. Some comparative data were obtained from young walrus that were reared in captivity in a temperate climate.

2. Internal temperatures of wild adults and calves were relatively labile, ranging from 34 to 39°C. Rectal temperatures of calves may have fluctuated in response to several factors, including teething, high air temperatures, and time of day. The mean rectal temperature of ten subadults and adults under natural conditions in -1 to 14°C air was 36.6°C.

3. Skin temperatures on the body during immersion were within 3°C of water temperature but rose rapidly to higher levels after emergence and drying. In general, the flippers warmed more rapidly than the skin of the body and attained somewhat higher temperatures.

4. The skin and flipper temperatures of calves in still air and shade did not rise continuously with increasing ambient temperature, but leveled off between air temperatures of 0 and 15°C and then rose again under warmer conditions. The upper limit of skin and flipper temperatures in the plateau were about 32 and 37°C, respectively.

5. The breathing rates of calves were highest at air temperatures near 0°C. They declined to a minimum at 15°C and rose again at 18°C. Brief periods of apnea were most common in air warmer than 10°C. The minimum heart rate occurred at 18°C.

6. Temperature gradients in the skin, blubber, and outer muscles were about five times longer than those in young harbor seals under comparable conditions. This difference was correlated with the greater thickness of the skin and blubber in the walrus. Gradient length is as much a function of the thickness of insulation as of the internal temperature-skin temperature difference. It is not a function of air temperature when the walrus is dry and is affected by other factors such as insolation.

7. The estimated lower limit of thermoneutrality (critical temperature) of the calves in still air and shade is about 5°C; in adults it is probably lower than -20°C. Adults are assumed to be thermoneutral when at rest in the water.

8. The estimated upper limit of the zone of thermoneutrality for isolated calves and adults is about 18°C in still air and shade or its equivalent under natural conditions. Animals in these or warmer conditions showed elevated skin, flipper, and body temperatures, as well as cutaneous hyperemia, restlessness, and fanning. Ultimately, they avoided further hyperthermia by withdrawing into the water.

9. The weather in spring and summer at the southern edge of the walrus' geographic range is often warm enough to induce hyperthermia and withdrawal to the water at a time when basking may be particularly important, especially during annual molt. Without physiological acclimatization and some major alterations of their more stable behavioral characteristics, such as diurnal inactivity, heliophilism, and huddling (which are adaptive for cold climates and not for warmth), walrus probably would not or could not occupy areas with warmer weather.

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